Observations on the Life Cycle and Flight Dispersal of a Water Beetle, *Tropisternus ellipticus* LeConte, in Western Oregon

(Coleoptera: Hydrophilidae)

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Species of the genus *Tropisternus* Solier are well known for their vagility (Spangler, 1960), but no detailed studies of flight dispersal have been made. In western Oregon, *Tropisternus ellipticus* LeConte can be collected from pond edges in the spring and fall, but disappears from ponds during summer. In 1972, I first collected this species from temporary rock pools along the Illinois River in southwestern Oregon. Since then I have found them in similar habitats along the Umpqua, South Santiam, and Willamette Rivers. This report describes the flight movements of *T. ellipticus* within and between habitats and relates dispersal movements to changes in reproductive state.

Beetles of the genus *Tropisternus* occur throughout the Western Hemisphere, generally in quiet water habitats. *T. ellipticus* is a dark green, broadly ovate, vertically elliptical beetle 8–11 mm long with a metasternal keel extended posteriad into a sharp point below the abdomen. As with other members of the genus, this species stridulates when seized (Ryker, 1972). Females fasten silken egg cases onto objects below the water surface, and the larvae are predaceous on small aquatic insects. Pupation occurs in moist soil. Adults graze and scavenge under water, consuming algae, detritus, and animal remains (Young, 1958).

Flight dispersal of Hydrophilidae has been simply summarized as spring dispersal flights, with the development of the next generation being completed in the summer, and a fall dispersal flight of newly emerged adults (Leech, 1956; Miller, 1963). Landin (1968) and Landin and Stark (1973) reported daily summer flights of *Helophorus brevipalpus*, a small hydrophilid in Sweden, and suggested that this species has both migratory and non-migratory flights.

Johnson (1970) hypothesized that insect migratory flight generally occurs in reproductively immature adult insects. He defined "migrations" as insect flights characterized by an exodus from one habitat, by undistracted or persistent flight, and by the location of a new acceptable habitat. Shorter flights resulting from the stimuli of changing micro-environmental conditions are "trivial" flights (Southwood, 1962).

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Following Chapman (1969), a period of adult reproductive delay or quiescence is referred to here as reproductive diapause.

FIELD STUDY LOCATIONS AND METHODS

Dispersal movements were followed by marking and releasing adult beetles inhabiting a series of rock pools at Waterloo Falls, South Santiam River, Linn County, Oregon and by year-round collecting from ponds in the Willamette Valley. Rock pools form in late spring (May, 1973 and June, 1974) as the summer dry period begins and the river recedes. They are covered again by the rising river when the winter rains begin in October. Pools that form in low spots during the winter rainy season and dry up in the spring will be referred to as winter pools.

The Waterloo rock pools were mapped and the number and location of each beetle captured was recorded. Using a No. 2 insect pin and a stereomicroscope, a number was scratched into the right elytron. Beetles marked and held in the laboratory showed no increase in mortality. The marks were permanent and did not become obscured, even after several months. Marked beetles were released within a few feet of their capture location. Beetles were collected either by netting swimming individuals or by removing floating *Spirogyra* mats and feeling for the beetles. All pools were sampled on each visit.

Beetle age was estimated as they were marked. In newly emerged, teneral beetles, a scratch would puncture the elytron and draw blood. Punctured beetles survived, however, and many were recaptured. Beetles about one week old could withstand a light scratch; beetles two and three weeks old were hard enough for careful marking; and beetles four weeks and older were quite hard and durable. Older beetles have a darker cuticle, scars, worn claws, and often have missing appendages and *Ceratomyces* fungi (Laboulbeniaceae) (Spangler, 1960) on the abdomen or between the claws.

To observe the movement of adult *T. ellipticus* to ponds in the fall, a small pond located at Peavy Arboretum near Corvallis, Oregon (20 miles west of the Waterloo site), was sampled regularly from September to December, 1973. Beetles were collected with an aquatic net from the pond perimeter for one hour per sampling day. Peavy pond was also sampled intermittently during winter and spring (1973–74) and summer (1972).

RESULTS

Observations on the movements and reproductive state of *T. ellipticus* will be presented seasonally, starting with winter. No beetles were found

when Peavy pond was sampled in December, 1973. When next sampled, on March 20, 1974, four specimens were collected. On March 21, 34 specimens were collected from the edge of the pond. This was following a period of five sunny days. Beetles were also collected from this and other permanent ponds in succeeding days in March and April. By May, 1974, adults were appearing in temporary pools at the Waterloo site and were becoming scarce in Peavy and other local, permanent ponds.

Overwintered adults were found breeding in the spring before the river had fallen enough for rock pools to form. On May 10, 1973, egg cases, third instars, and some very dark, scarred and parasitized adults were collected in two temporary winter pools just above the Waterloo rock pool area. Overwintered adults did not appear in rock pools in 1973 and were not found in ponds after the end of May, which suggests that they died after spring breeding. In 1974, overwintering adults were seen flying between April 29 and June 16 and collected at Waterloo from temporary winter pools and several high rock pools that formed in April and were dry by June. A female, marked in a rock pool August 12, 1973 and about 10 months old, was collected in a winter pool at Waterloo on May 8. Egg cases were present at this time, and four overwintered females dissected had developing eggs in their ovaries.

Beetles that immigrated into newly formed river rock pools at Waterloo in May, 1973 (Fig. 1) were of the spring generation (bright green, not fully hardened, undamaged, not parasitized) and not of the overwintered generation. In 1974, spring rains delayed the formation of the Waterloo rock pools until June. New generation beetles that appeared then were already hardened, and four of five females dissected June 10 had small, partially developed eggs, and the abdomen full of fat body. The fifth female had about one-fourth of her eggs fully developed, and much less fat body. About half of the beetles collected on June 10 ($n = 48$) were new generation adults, and by June 29 adults of the overwintering generation were no longer found.

Teneral adults (< 2 weeks old) appearing in the Waterloo rock pools in 1973 were counted, and the number captured per sampling day is shown in Fig. 1. A large influx of teneral beetles occurred in mid-May, but the percentage (of beetles collected per sampling day) that was teneral dropped to zero on May 28 ($n = 37$). Subsequently, teneral adults appeared in samples throughout the summer.

Four teneral beetles collected from rock pools were dissected August 1–4, 1974, to see if they were reproductively mature. They were found to have undeveloped ovaries and no noticeable fat body. Six hardened

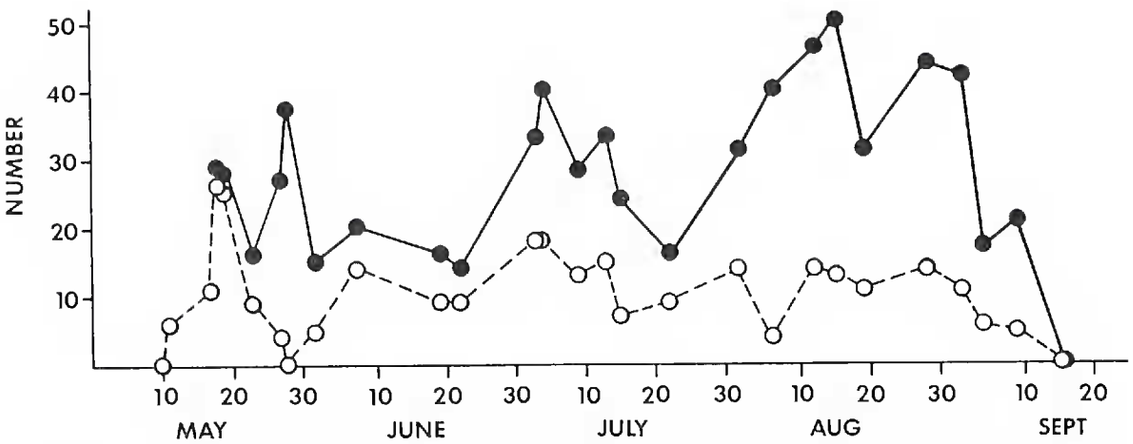

FIG. 1. Number of teneral adults (dashes) and total number of *Tropisternus ellipticus* adults captured at Waterloo, Oregon in rock pools during summer, 1973.

adult females collected from rock pools at the same time were dissected and found to contain eggs. The eggs were fully developed, filling the abdominal cavity, and very little fat body was present.

Twenty-two beetles were observed flying and entering pools in 1974. These flights were observed on warm, cloudless days between 11 AM and 3 PM. Of these flights, two overwintered adults were taken entering a sandy pool on April 29. Ten beetles on June 10, one on June 12, and nine on June 29 were taken entering rock pools. The beetles flew slowly into the breeze at one to two meters height and often circled back after crossing a pool, sometimes hovered briefly, and then closed their elytra and fell. Beetles observed flying at midday across small pools fell at the north edge of the pool, sometimes hitting on the rock edge and scrambling for the water.

Both sexes moved in and out of the Waterloo rock pools throughout the summer. Of 487 beetles marked and released, 140 (29%) were recaptured. Recaptured individuals were captured an average of 2.5 times. Thus the beetles tended to fall into two classes—those that were captured only once (71%) and those that settled into the pools and moved short distances only. Some of these were captured five or six times over a period of several months. Of the beetles recaptured, 26% had changed pools. However, of 28 beetles recaptured within two days, 27 (96%) were still in the same pool, but often at a different location within the pool. Beetles were often captured in the same pool several times over a period of several weeks if the pool did not dry up or become flooded with cold river water.

Pools containing beetles between July 9 and August 1, 1973 had a temperature range of 23° to 33° C ($\bar{x} = 28.7 \pm 0.24$° C; $n = 114$ beetles). Unselected pools had temperatures ranging from 14° to 35° C.

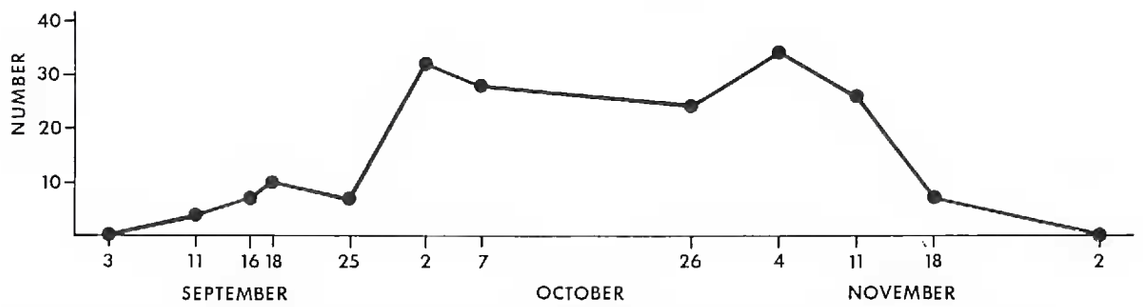

FIG. 2. Destructive sampling for *Tropisternus ellipticus* from a small pond at Peavy Arboretum, Corvallis, Oregon, 1973. Each sampling period was one hour.

One pool, which never yielded specimens, consistently had cool temperatures (14°–20° C). In June and July, 1973, beetles left pools that were drying up and therefore very warm (> 33° C), or pools with water temperatures below 21° C for several days. However, after August 5, the river level rose and all pool temperatures fell below 22° C. Beetles were found in this colder water until mid-September.

Adult females collected in early summer and held in the laboratory usually laid eggs within three days, but females collected at Waterloo August 15, 1973 and held with males in an observation pool for three weeks did not produce eggs. Egg cases had been observed at Waterloo throughout the summer, but by August 28 no cases containing eggs could be found. However, third instars (> 2 weeks old) were still present in some pools, and the adult population was present (Fig. 1).

In early October, 1972 and in mid-September, 1973, the number of adult *T. ellipticus* collected at the Waterloo site fell to zero (Fig. 1), suggesting that the adults had begun migrating. Concurrent with this decrease, adults began to appear in samples at Peavy pond (Fig. 2), presumably migrating from rock pools nearby. I have found *T. ellipticus* in rock pools but not in permanent ponds from June through August in nine years of collecting *Tropisternus* in western Oregon. Other species are present in ponds during the summer, however. Data from museum specimens at Oregon State University also indicates that *T. ellipticus* is found in ponds from September through November and from February through May, but no specimen labels (except mine) have summer collection dates.

Six females collected from ponds and dissected in October had undeveloped ovaries, and the abdomen was full of fat body. Beetles collected from ponds in the fall were paired in pint jars under conditions found to be favorable for laboratory rearing in the summer, and observed for indications of reproductive diapause. With one exception, 30 male-female pairs held under several sets of light and temperature conditions

for a minimum of 25 days did not breed. One female produced a single egg case, and she had been paired with a male under long days and temperatures fluctuating between 20° C at night and 27° C during the daytime. This pair, however, produced no more eggs in the concluding 30 days of the trial.

To see if diapausing adults lose their ability to fly after reaching the ponds in the fall, males and females collected in September and held at 16° C for five months were tested for flight ability. All ten males and eight of ten females flew up out of a Petri dish in response to a 250 W lamp. These beetles were paired subsequently under favorable rearing conditions to be certain that they were diapausing, and none of the pairs produced eggs.

Tropisternus adults are difficult to find in winter. Fig. 2 shows that *T. ellipticus* disapeared from the edge habitat in Peavy pond in late November, 1973. Spangler (1960) suggested that they may overwinter buried in the bottom mud or in pond edge soil. Accordingly, a habitat choice test was set up to see if these beetles will bury themselves in moist sand or in bottom mud. Seventeen beetles collected in September from Peavy pond were held at 16° C (8L/16D) in an aquarium that had sand extending from the bottom to 15 cm above the water level at one end, flat rocks on bottom mud, and floating aquatic vegetation. After 30 days, two beetles were still in the aquatic vegetation, six were buried in sand above the water level, and nine were buried beneath the flat rocks on the mud bottom. I have collected occasional specimens from pond bottoms in winter, and a few from beneath flat rocks at pond edges, but have not excavated pond edges to see if they burrow into the soil there.

DISCUSSION

Adults of *T. ellipticus* disappeared from the edge habitat of permanent ponds in western Oregon in late November, 1973, and reappeared in March, 1974. Overwintered beetles were dispersing into temporary winter pools in early spring before the rock pool complexes along the S. Santiam River were uncovered. The appearance of overwintered adults, eggs, and larvae in winter pools and recently-formed pools at Waterloo by late April and early May in both years indicates that they had resumed breeding.

Teneral progeny of the overwintered beetles appeared in May, 1973, and hardened progeny in June, 1974, migrating into the newly-formed rock pools. Although no specimens were dissected in May, teneral adult females dissected in early August, 1974, had undeveloped ovaries.

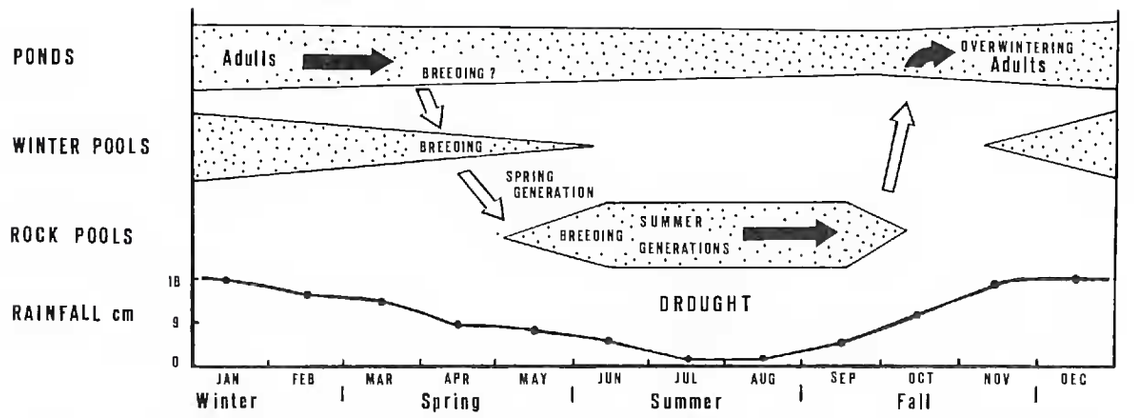

FIG. 3. Aquatic habitats used by *Tropisternus ellipticus* in western Oregon and normal precipitation for Waterloo, Oregon (Climatological Data, Oregon Annual Summary, 1973, U.S. Dept. Commerce).

Ovaries were beginning to develop in the June, 1974 individuals, but the eggs only partially filled the abdomen. Hardened females dissected in mid-summer had abdomens filled and distended with eggs. It seems probable, then, that the spring migration into rock pools primarily consists of reproductively immature adults.

Overwintered individuals were no longer found after mid-May in 1973 and late June in 1974. The new generation bred in the rock pools until mid-August, 1973, producing teneral individuals continuously until September. Continuous breeding, immigration, and inter-pool movements obscured the distinction between one or more summer generations. The laboratory rearing time for this species is about 45 days (unpublished data). This, theoretically, gave *T. ellipticus* time to produce a second generation by July in 1973, and by August in 1974, with both generations reproducing until mid-August. Third generation adults did not have time to breed during their first summer because they could not have eclosed before late August or September, after breeding had ceased.

All adults left the rock pools in the fall, but it is not known whether only the second and third, or both the summer generations and the spring generation migrate and survive the winter to resume breeding the following spring. The only marked beetle recaptured after overwintering probably had eclosed in late July as a second generation beetle.

Adults ceased breeding in the rock pools in mid-August, 1973, although they did not emigrate for another month. The female abdominal cavity, filled with eggs in the summer, was packed with fat body in the fall. Because efforts to induce adults to breed in the fall and early winter failed, in contrast to successful maintenance of breeding pairs in the summer, I feel that they are in a state of reproductive diapause.

Coincidence of the phenomena of emigration from rock pools and the appearance of *T. ellipticus* in ponds is good circumstantial evidence that this species migrates from rock pools to ponds in the fall in western Oregon. The beetles disappear from pond edges in early winter. The laboratory habitat choice test indicated that the beetles are capable of burying themselves in the bottom mud or in soil, and may do so in the pond habitat, as was suggested by Richmond (1920) and Spangler (1960). Occasional collection of specimens from pond bottom mud also supports this idea.

Besides spring and fall migratory flights and the dispersal movements of overwintered adults in April and May, intermittent trivial flights of individuals occurred in the river rock pool habitat during the summer. These movements apparently were responses to ponds either drying up and becoming too warm, or being flooded by cold river water. The most frequented pools were close to 29° C in midafternoon, about 10° C warmer than the river.

Observations of flights of *T. ellipticus* are similar to those mentioned by Zimmerman (1959) for *Tropisternus lateralis nimbatus* and those of *Helophorus* (Landin, 1968; Landin and Stark, 1973; Fernando, 1958) in that they occur during the daytime. However, these observations differ in that *T. ellipticus* was observed flying upwind, whereas the smaller *Helophorus* may be wind-borne. *T. ellipticus* often fell to the north edge of small pools at midday, and may have been responding to the image of the sun reflected from the still water surface.

T. ellipticus has three of the types of flight dispersal mentioned by Johnson (1970): 1) migration of teneral adults from one habitat to another; 2) trivial dispersal flights by individuals from one place to another within a habitat in response to fluctuations of microenvironment; and 3) migration of diapausing adults from one habitat to another. Previous generalizations about Hydrophilidae (Leech and Chandler, 1956; Miller, 1963) suggest that spring dispersal flights are of overwintered individuals and that fall flights are of "newly emerged" individuals. However, although the overwintered generation of *T. ellipticus* disperses in early spring and can be found breeding in winter pools, the late spring migration is of new generation, often teneral adults, and the fall migration is of non-teneral, diapausing adults.

Pajunen and Jansson (1969) showed that rock pool Corixidae in Finland have physiological and behavioral adaptations, similar to *T. ellipticus*, which allow them to breed in summer in temporary pools and to overwinter as diapausing adults in deeper pools. Ova of overwintering

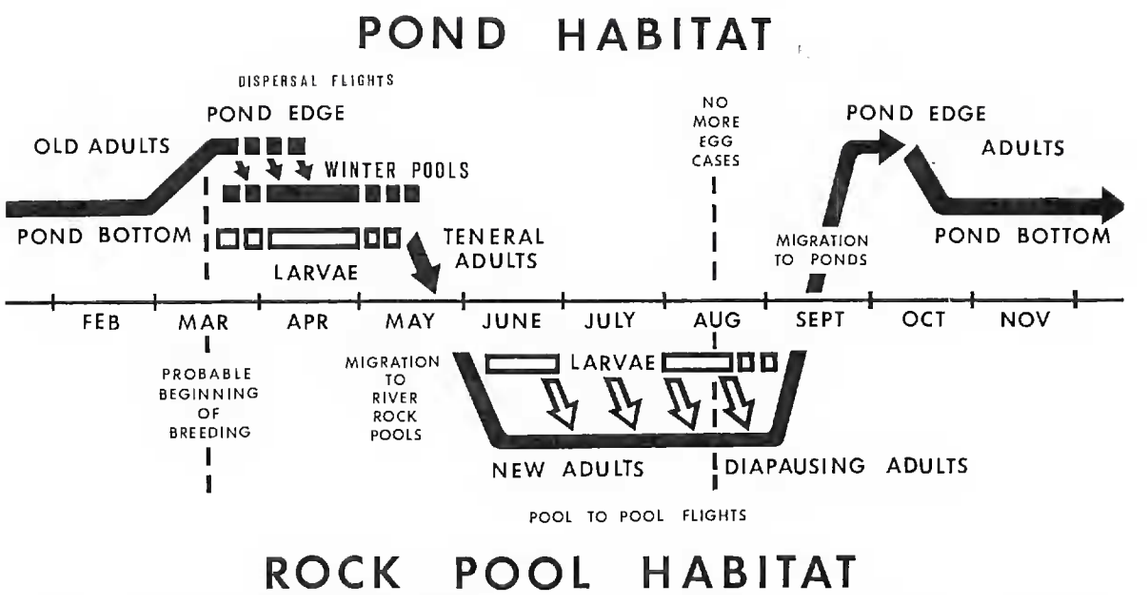

FIG. 4. Life cycle, flight dispersal, and habitat selection of *Tropisternus ellipticus* in western Oregon.

adults do not mature until after spring migration. These corixids fly to shallower rock pools for spring breeding, as does *T. ellipticus* for summer breeding, and they have a similar pattern of summer dispersal flights of breeding adults between temporary pools. Migratory flights of both Corixidae and Hydrophilidae into and out of temporary rock pools are of teneral, immature, or partly mature adults (late spring), or of reproductively diapausing adults (fall). These observations agree with Johnson's concept that migratory flight characteristically occurs in reproductively immature adult insects.

Because old generation adults were seen flying on sunny days in early May and entering temporary winter pools and rock pools, an alternative description of habitat selection behavior by *T. ellipticus* is also plausible. These species may select pond habitats after entering reproductive diapause in fall, and select rock pools or the best substitute (winter pools) when reproductive maturity ensues. In this view, overwintered adults reassuming breeding condition in the spring tend to seek the rock pool habitat, except that rock pools are not available. When river levels drop, rock pools form, this event generally coinciding with eclosion of the new generation and demise of the old.

Wiggins, Mackay and Smith (1974) presented a concept of community organization for animals inhabiting annual temporary pools, making a distinction between vernal and autumnal pools. River rock pools are neither vernal nor autumnal pools because they appear during the summer drought. Winter pools in western Oregon are pools that are "temporary" from October to May during the winter rains, and are

functionally similar to vernal pools in the spring (Fig. 3). In the scheme of Wiggins et al., *T. ellipticus* is a Group II animal, a pool stage arrival adapted to temporary pools by evolution of dispersal behavior.

The main features of the life cycle of *T. ellipticus* in western Oregon are summarized in Figs. 3 and 4. Adults overwinter apparently in the soil or under bottom rocks of ponds. In early spring they move to the pond edge habitat, subsequently dispersing on warm days to other ponds and winter pools, where they breed in April and May. Their offspring, the spring generation, migrate (sensu Johnson) into the newly formed river rock pools and begin breeding. Offspring of spring generation adults, the second, or summer, generation, may have time to mature and breed in dry years like 1973, in which case their offspring would eclose in time to migrate to ponds before the rivers flood the rock pools. Adult female beetles stop producing eggs (reproductive diapause) in mid-August, and their abdomens fill with fat body. About a month later the surviving adults of spring and summer generations migrate from rock pools to the edge habitat of permanent ponds, and then move to the pond bottom or edge soil for the winter.

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